

GUTTURAL CALLS OF BLUE-FRONTED AMAZONS: STRUCTURE, CONTEXT, AND THEIR POSSIBLE ROLE IN SHORT RANGE COMMUNICATION

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ABSTRACT.—Structural variability of guttural calls of Blue-fronted Amazons (*Amazona aestiva*) was examined and the contexts in which they were given discussed relative to the role these vocalizations might play in short-range communication. Recordings were obtained at the Chancaní Reserve, Córdoba, Argentina, during breeding and non-breeding seasons. Guttural calls were given year round, but were more common during the non-breeding season when most of the individuals were interacting in flocks. Gutturals were detected when perched parrots contacted each other, during take-offs, landings, complex flock flying maneuvers, and feeding sessions. Guttural calls were subdivided into four types based on structure, but none of these types could be clearly assigned to a specific context. Structural variation in guttural calls was continuous rather than discrete, with the variability within and among individuals being similar. Many guttural notes graded into one another and were combined with other vocalizations. Gutturals were brief, had sudden onset, wide bandwidth, and low intensity. Gutturals could be regarded as short-range calls because of their large structural variability (fewer restrictions of sound attenuation and degradation) and low intensity (decreased attraction of predators). They were also produced by large flocks, probably as a means of maintaining contact, enhancing group spacing, and coordinating movements of individuals. *Received 11 Feb. 1999, accepted 19 Oct. 1999.*

Several parrot species have rather complex vocal repertoires (Farabaugh and Dooling 1996), with different vocalizations used in specific contexts (Saunders 1983, Martella and Bucher 1990, Fernández-Juricic et al. 1998a). They exhibit recognition of conspecifics (Rowley 1980, Saunders 1983, Wanker et al. 1998), vocal dialects (Wright 1996), and vocal mimicry (Cruickshank et al. 1993). Some call sequences structurally and functionally resemble passerine songs (Farabaugh et al. 1992, Fernández-Juricic et al. 1998c). Although previous studies have contributed to our understanding of parrot vocalizations, little is known about their structural variability or possible roles in social organization, particularly in wild populations.

The Blue-fronted Amazon (*Amazona aestiva*) is an interesting species because of its large structural and contextual vocal variability (Fernández-Juricic et al. 1998c) and its endangered status in many areas of its range (Bucher et al. 1992). Its vocal repertoire encompasses at least nine vocalizations, many of

which are produced in different contexts (Fernández-Juricic et al. 1998c). The most commonly uttered call is the *wakwak*, which is associated with several situations (alarm, flight, contact) and is given along with other vocalizations, such as *wawawawa*, transitions, *gugugu*, and gutturals. Guttural calls are variable in frequency and time, especially when used in close proximity to other individuals (Fernández-Juricic et al. 1998c); however, structure, variability patterns, and contexts of these vocalizations remain poorly known.

This study has three main purposes: (1) to analyze the structural variability of guttural calls, (2) to determine the contexts of vocalization, and (3) to evaluate the hypothesis that guttural calls may be used as short-range signals in the forest habitats of this species. Depending upon habitat structure, animal vocalizations may withstand attenuation and degradation (Morton 1975, Wiley and Richards 1982, Forrest 1994). In closed habitats, the acoustic adaptation hypothesis (Rothstein and Fleischer 1987, Brown and Hanford 1996) predicts that for long distance signals animals should use long tonal or whistled sounds and avoid repeated elements. Short-range communication signals are expected to show higher structural variability because of the fewer restrictions in environmental sound propagation channels (Marler 1967, Morton 1982).

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Other differences might include shorter duration, sudden onset, broader frequency range (Clemmons 1997), and low intensity to reduce auditory detection by predators (Wiley 1976, Wiley and Richards 1982). Short-range signals are predicted to function as contact calls because they are vocalized more frequently by interacting social units than by solitary individuals (Smith 1986, Mathevon 1997).

METHODS

Study area.—Samples of Blue-fronted Amazon guttural calls were recorded in the Chancaní Reserve, Córdoba, Argentina (65° 26' W; 30° 22' S), a 4920 ha area of Chaco habitat where the dominant plant community comprises the quebracho-blanco forest (*Aspidosperma quebracho-blanco*; Carranza et al. 1992). Annual precipitation ranges from 300–550 mm (Capitanelli 1979).

Approximately 50 individuals inhabit the reserve, which appears to be isolated from other suitable forest patches and are at the southern limit of the species' range (Fernández-Juricic et al. 1998b).

The reserve was visited five times during 1993 and 1994. Sampling was concentrated in the morning (from 30 min before sunrise to mid-morning) and afternoon (in the 3 h before sunset), resulting in 100 hours of observation (10 recording h), using the techniques of Altmann (1974).

Vocalizations and sonograms.—Vocalizations were recorded with an Uher 4000IC tape recorder at a speed of 19.05 cm/s and a directional microphone (Electro-Voice Model 644). A 16-bit stereo Sound Blaster card was used to digitize sounds up to 22.05 kHz. Sonograms were made with Spectrogram 2.3 software, with broadband analyses [FFT window width: 12 milliseconds (ms)]. The following structural variables were measured (Fig. 1): low frequency [the lowest frequency record in the sonogram, in Hertz (Hz)], high frequency (the highest frequency record in the sonogram, in Hz), frequency range (bandwidth, the difference between the highest and lowest frequencies, in Hz), energy concentration (the frequency at which the acoustic energy is strongest, in Hz), number of harmonics (number of frequency band multiples of the fundamental), number of frequency modulations, and duration (in ms).

Because Blue-fronted Amazons were sexually indistinguishable and the threatened status of the Chancaní population did not allow tagging individuals, we could not reliably distinguish between individuals. To estimate inter-individual acoustic variability and to reduce the effects of pseudoreplication (Hurlbert 1984), we proceeded as follows: recordings were primarily made when birds were flying to feeding grounds and roosting areas; when feeding; when arranging cavities to be used as nests; when perching before, during, and after social interactions; and when fleeing from intruders (such as the observer). Flocks were identified, mapped,

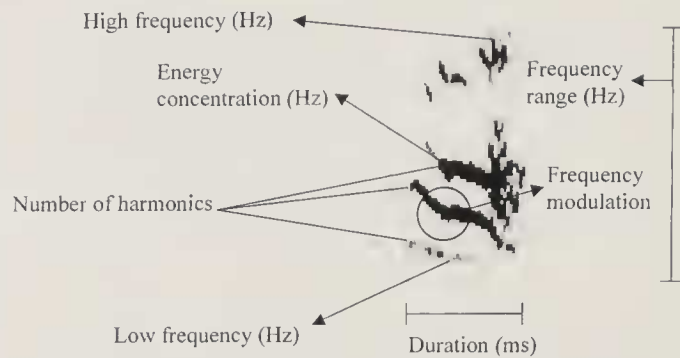


FIG. 1. Structural traits measured on Blue-fronted Amazons (*Amazona aestiva*) guttural calls: low frequency [the lowest frequency record in the sonogram, in Hertz (Hz)], high frequency (the highest frequency record in the sonogram, in Hz), frequency range (bandwidth, the difference between the previous variables, in Hz), energy concentration (indicates the frequency where most of the acoustic energy is concentrated, in Hz), number of harmonics, number of frequency modulations, and duration (in ms).

and acoustically sampled in distinct recording bouts. Each bout was assigned to a specific flock so that we could identify bouts from different groups that were not overlapping. From each of these different flock bouts, we collected only one guttural call belonging to one individual from each group for statistical analysis. This procedure was repeated throughout the study period so as to get a similar number of guttural calls for each sampling period and day, and as many different guttural calls as possible (total sample size = 80 calls). Hence, the sampling unit was a single individual within a flock, regardless of the number of individuals within the flock. This method reduced the probability of taking multiple samples from the same individual and biasing the results. A similar selection procedure was used to analyze the other vocalizations used for comparison.

Although intra-individual variability could not be estimated because of the restriction against tagging individuals, we made a rough estimate. On two consecutive days in four different zones of the reserve, we were able to record several guttural calls belonging to four different parrots (19, 15, 11, and 14 calls, respectively). All four parrots were recorded within flocks of at least four individuals. The variability within the calls of these four parrots was then compared to that among individuals (35 notes randomly selected from the pool of 80 calls) by a test for differences between variances (Sokal and Rohlf 1981), by which $F = S_1^2 / S_2^2$, with $(n_1 - 1)$ and $(n_2 - 1)$ degrees of freedom, and S_1^2 and S_2^2 were the larger and the smaller variances, respectively. Although the estimate of intra- vs inter-individual variability could have been biased because of a small sample size, our intention was to assess whether the variability in guttural calls stemmed from intra-individual variability (individuals using different vocalizations) or inter-individual variability (each individual using a single vocalization).

TABLE 1. Structural features of 80 Blue-fronted Amazons' guttural calls recorded in the Chancaní reserve, Córdoba, Argentina. Frequency variables are expressed in Hz, and duration in ms.

	Low frequency	High frequency	Bandwidth	Duration	Concentration of acoustic energy	Number of harmonics	Number of frequency modulations
Mean	634.46	3447.35	2813.51	126.50	1771.61	4.56	4.31
SD	238.37	973.83	1077.84	33.73	263.91	1.72	2.44

Structural and contextual analysis.—Guttural calls were first characterized by mean and standard deviation (SD) of the acoustic traits (Fig. 1). A Principal Components Analysis (PCA) was performed to generate a reduced set of variables that account for most of the variability in the original data set. Low and high frequency were excluded from the analysis because they were highly correlated with bandwidth. We employed a correlation matrix because variables were on different measurement scales. Only those PCA factors with eigenvalues greater than 1 were selected (Kaiser criteria; StatSoft, Inc. 1996). The factors identified by the PCA were then used to assign guttural calls to one of four arbitrary types (corresponding to the four quadrants determined by the arrangement of the two first classification factors). We also examined the other PCA factors for grouping of gutturals. Each guttural call type identified was then related to the contexts of vocalization.

The following terms were adopted to describe the calls (Fernández-Juricic et al. 1998e): note, a short sound not interrupted by a silence; complex syllable, a group of different notes encompassing coherent units in the sonogram; bands, frequency sectors in which acoustic energy is concentrated; and transitions, a note with less intensity in relation to other guttural calls given at the same distance as indicated by a fainter trace in the sonogram.

Guttural calls were compared with six other types of calls (*wakwak*, *wawawawa*, transition to *wakwak*, *gugugu*, *grruúp*, and songs; described in Fernández-Juricic et al. 1998e) with corrected coefficients of variation because of low sample sizes ($CV' = (1 + 1/4n) \times CV$) and a test for differences between variances (Sokal and Rohlf 1981). The following traits were considered in the comparisons: energy concentration, high frequency, and low frequency.

An ANOVA was employed to analyze mean duration and bandwidth of guttural calls with regard to four calls: *wakwak*, *wawawawa* (structurally different and frequently used in alarm situation), *gugugu*, and songs (structurally similar to gutturals, but employed over long distances). Residuals of the analysis were normally distributed and had equal variance.

Guttural call amplitudes were compared by *t*-test with the most common Blue-fronted Amazon vocalization: *wakwak*. Call intensity [decibels (dB)] was measured with the software Wave Editor 1.03. Because intensity can be highly biased by attenuation/reverberation effects produced by slight differences in recording distances (Wiley and Richards 1982), we included

in the analysis recordings taken at 100 ± 5 m from the source (usually flying parrots).

To analyze whether gutturals would be playing a more relevant role in the transmission of information at short distances as the number of interacting individuals increased, we assessed the variability in five structural properties of guttural calls (low frequency, high frequency, bandwidth, energy concentration, and duration) in flocks of 1, 2–3, and more than 4 individuals by means of the same test for differences between variances discussed before (Sokal and Rohlf 1981). All statistical analyses were conducted with STATISTICA 4.5 software.

RESULTS

Structural characteristics.—Guttural calls consistently share five characteristics: short duration, high structural diversity (several structurally different notes), frequency modulation (most analyzed frequency bands showed upward and downward shifts), broad bandwidth, and sudden onset (Table 1, Fig. 2). Structurally, gutturals were highly variable and included notes that were modulated over a wide frequency range either upwards or downwards (Fig. 2A–C), notes slightly modulated (Fig. 2D–F), complex and long-duration notes (Fig. 2G), buzz sounds (Fig. 2H), barely audible sounds (Fig. 2I), short notes with blurred or noisy frequency structure (Fig. 2J), and complex syllables composed of two distinct units (Fig. 2K).

The Principal Component Analysis generated two components that accounted for nearly 76% of the observed variance (Table 2). The first factor was composed of bandwidth, number of harmonics, and number of modulations; the second factor included the concentration of acoustic energy (Table 2). Guttural calls were assigned to one of four types according to their positions in the four quadrants produced by the PCA axes (Fig. 3; Q1, Q2, Q3, and Q4). Axes beyond PC1 and PC2 were not important for grouping guttural calls. Most guttural notes (Q1 and Q3) seem to have narrow bandwidths with little modulation

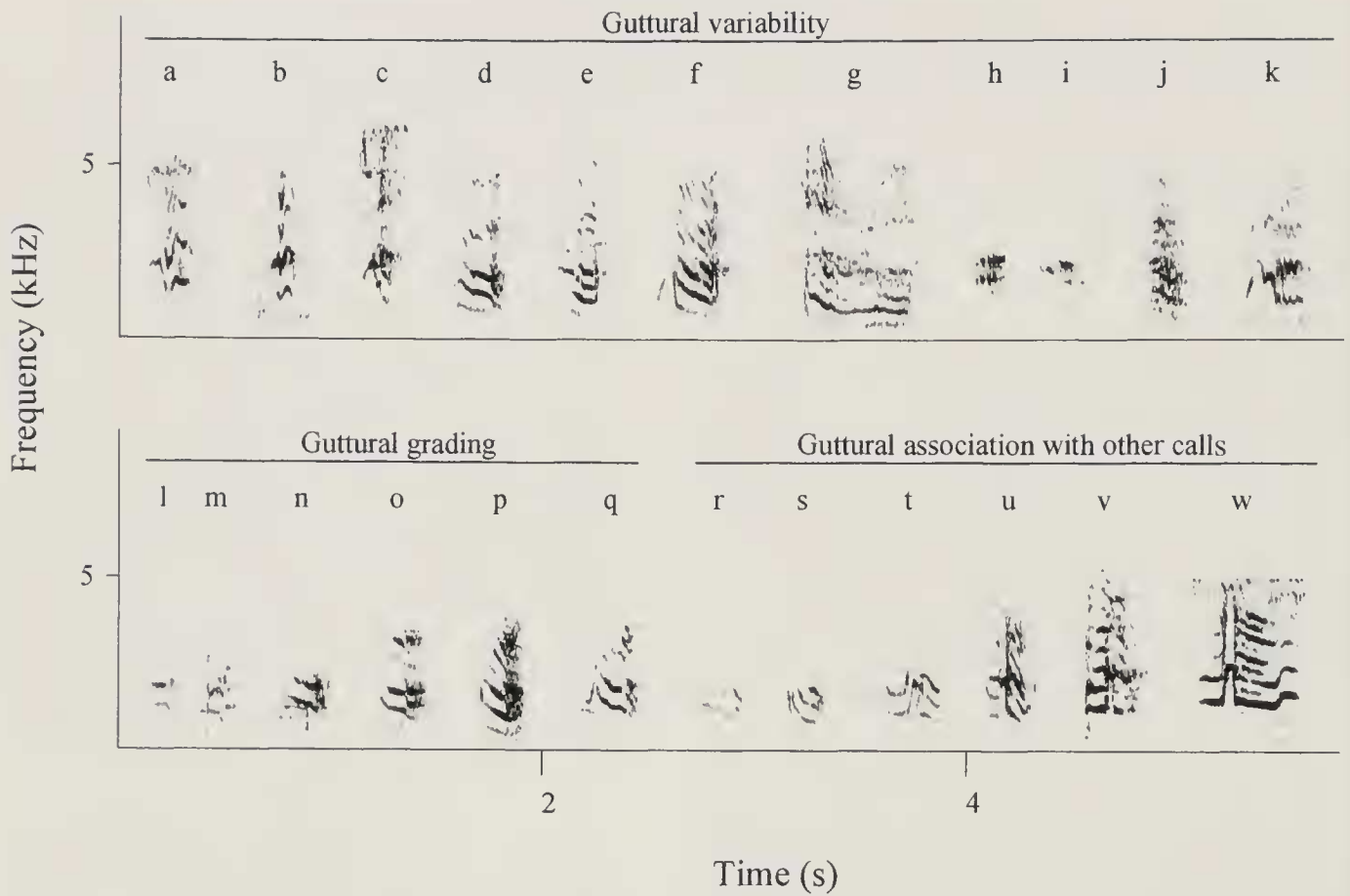


FIG. 2. Guttural calls of Blue-fronted Amazons (*Amazona aestiva*) recorded in the Chancaní Reserve, Córdoba, Argentina. Calls given when perching or taking off but not during flights (A–C), calls produced by flying or perching parrots (D–F), calls given by isolated individuals contacting a large flock, during coordinated take-offs, and while perching (G–K), a sequence depicting a simple graded bout of gutturals given by a single individual (L–Q), sequence (R–W) showing the association between gutturals (R–S) and other Blue-fronted Amazon calls: transitions to *wakwak* (T–U), and *wakwaks* (V–W).

(Fig. 2D–F). Much of the overall structural variation appears to be continuous rather than discrete (Fig. 2), resulting in no clustering of notes (Fig. 3).

Intra- vs inter-individual variation.—The structural variability of guttural calls within

and among individuals was similar (Fig. 4). Eighty percent of the multiple variance comparisons were not significant ($F_{10,34} = 1.048–2.083, P > 0.05$); only four contrasts showed that the variability among individuals (G) was

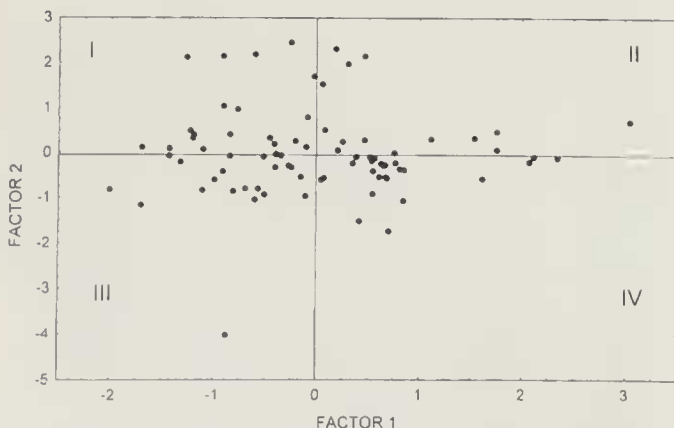


FIG. 3. Individual guttural calls of Blue-fronted Amazons (*Amazona aestiva*) and their positions along the first two Principal Component axes.

TABLE 2. Correlations between the first two Principal Components and the original variables of 80 guttural calls of Blue-fronted Amazons *Amazona aestiva*. Significant correlations ($P < 0.05$) among variables and factors are marked with *.

	Factor 1	Factor 2
Bandwidth	0.873*	0.003
Duration	0.654	–0.224
Energy concentration	–0.025	–0.980*
Number of harmonics	0.905*	0.098
Number of modulations	0.863*	0.036
Eigenvalue	2.75	1.02
Variance (% total explained)	55.09	20.47
Cumulative Variance (%)	55.09	75.56

TABLE 4. Coefficients of variations of seven Blue-fronted Amazons' vocalizations considering four structural traits: energy concentration, high frequency, bandwidth, and duration.

Vocalization	High frequency	Bandwidth	Energy concentration	Duration
<i>wakwak</i>	76.2	100.1	29.8	177.4
<i>wawawa</i>	78.9	90.5	74.2	134
transitions	52.9	81.5	17.3	108.1
<i>gugugu</i>	37.6	59.8	24.6	132.9
<i>kakaka</i>	236.3	276.4	101.6	306.4
<i>gruip</i>	28.7	35.9	12.8	42.2
Guttural calls	671.5	1021.1	439.7	747.1

paring the variances of the three frequency features (low frequency, high frequency, and bandwidth), guttural variability was greater (Table 5).

Guttural calls were briefer than *wawawawa*, *wakwak*, *gugugu*, and songs (ANOVA: $F_{4,126} = 39.15$, $P < 0.001$; guttural calls, 135.4 ± 40.5 ms; *wawawawa*, 353.9 ± 79 ms; *wakwak*, 243.2 ± 50.8 ms; *gugugu*, 253.2 ± 84.1 ms; songs 153.8 ± 100.8 ms); the latter four were frequently used for contact over long distances (Fernández-Juricic 1994). The bandwidth of gutturals was intermediate, larger than *gugugu* and songs (ANOVA, $F_{4,126} = 166.4$, $P < 0.001$; guttural calls, 3687.8 ± 603 Hz; *wawawawa*, 4805.3 ± 725.3 Hz; *wakwak*, 4802.5 ± 565.9 Hz; *gugugu*, 1405 ± 210 Hz; songs 1828.3 ± 542 Hz). Gutturals were also softer than the commonly uttered *wakwak* calls ($t = 13.143$, 42 df, $P < 0.001$: gutturals, 0.36 ± 0.03 dB; *wakwak*, 0.91 ± 0.02 dB).

The variability in guttural call duration and lowest frequency was greater for flocks larger than four individuals than for single individ-

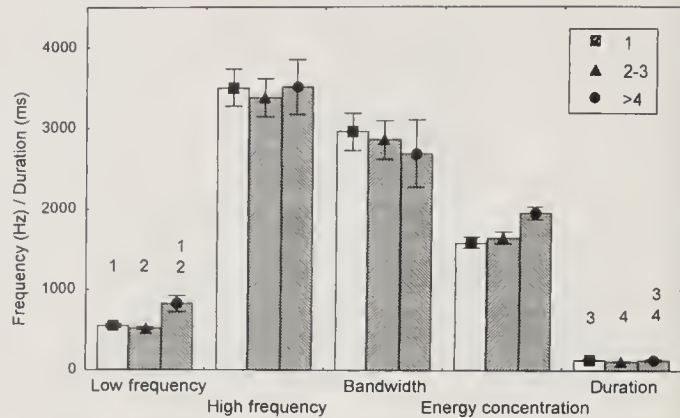


FIG. 5. Acoustic variability in guttural calls of Blue-fronted Amazons (*Amazona aestiva*) in relation to flock size categories (1, 2–3, more than 4 individuals, 15 randomly selected notes per category). Columns with the same number indicate pairs of significantly different contrasts: more than 4 vs 1, low frequency, $F_{14,14} = 4.02$, $P < 0.01$; more than 4 vs 2–3, low frequency, $F_{14,14} = 5.93$, $P < 0.01$; more than 4 vs 1, duration, $F_{14,14} = 2.7$, $P < 0.05$; more than 4 vs 2–3, duration, $F_{14,14} = 2.57$, $P < 0.05$.

uals (Fig. 5). Low frequency and duration were the structural variables included in the significant contrasts (Fig. 5). The other traits (high frequency, bandwidth, and energy concentration) did not show any significant difference among different sized social groups ($F_{14,14} = 0.678-1.792$, $P > 0.05$; Fig. 5).

DISCUSSION

Guttural calls can be regarded as highly variable. This variability apparently increases with flock size, with single individuals producing notes as different as those given by all the other flock members. Variability in parrot contact calls has also been described for *Amazona auropalliata*, in which geographic dif-

TABLE 5. Comparison of the variation in guttural calls and other Blue-fronted Amazon vocalizations. Sample sizes: guttural = 80, *wawawawa* = 20, *gugugu* = 12, *kakakaka* = 62, transition = 9, *wakwak* = 30, *gruip* = 8. Shown are F values and significance levels of tests for differences between variances (Sokal and Rohlf 1981).

Comparison	Energy concentration	High frequency	Low frequency
Guttural– <i>wawawawa</i>	2.491 (*) ^a	3.387 (**)	3.937 (***)
Guttural– <i>gugugu</i>	11.479 (***)	36.391 (***)	9.226 (***)
Guttural– <i>kakakaka</i>	18.272 (***)	3.108 (***)	2.090 (**)
Guttural–transition	11.601 (***)	3.140 (*)	14.251 (***)
Guttural– <i>wakwak</i>	25.995 (***)	7.524 (***)	3.391 (*)
Guttural– <i>gruip</i>	39.015 (***)	4.672 (*)	4.049 (*)

^a * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

ferences are reflected in the acoustic properties of these calls (Wright 1996).

The results of this study further characterize guttural calls in structural terms: within and among individual variations are similar, some notes appear to grade into each other, gutturals are combined with other vocalizations in a specific order, and structural categories cannot be exclusively ascribed to specific contexts. No definite conclusion could be made to account for such structural variability, and further analyses are needed (particularly by means of playback tests). However, some preliminary conclusions (not mutually exclusive) can be drawn.

First, the structural variation in guttural calls might be associated with the transmission of different messages. In this case, specific structural variations would be associated with particular messages (Hailman et al. 1987, Smith 1997). Although some guttural types were more frequently recorded in specific circumstances, most types were given in all contexts. Second, different guttural calls might represent different functional categories. If so, each guttural type would have structural variation similar to other vocalizations of the Blue-fronted Amazon's repertoire (*wakwak*, *wawawawa*, etc.). However, the continuous variation in gutturals, along with the lack of complete specificity, indicates that these two hypotheses are not supported with the information available. Third, the degree of variation in guttural calls might result from the acoustic restrictions of short range communication (discussed below).

Variability in guttural vocalizations seems to be continuous rather than discrete. A continuous variability might allow individuals to take advantage of the situational context to support the behavioral message of the call (Morton 1982, Smith 1986). Such contextual variation could support different amounts of information within single or multiple calls (Marler et al. 1992, Armstrong 1995, Smith 1997). Thus, Blue-fronted Amazons might rely on contextual information because the guttural call types lack specificity.

Guttural types do not appear to be functionally distinct. The continuous variability of gutturals coupled with the variety of contexts in which they were given suggest that these vocalizations are a single acoustic and func-

tional category that may serve to maintain vocal contacts among Blue-fronted Amazons. Guttural calls were more frequent during the non-breeding season, presumably as a result of larger and more dynamic flocks which, consequently, produced more interactions among individuals (Fernández-Juricic et al. 1998b). Thus, parrots might rely upon gutturals to inform other flock members of conditions when moving and foraging as a cohesive group (Smith 1986, 1997; Boughman 1997). Moreover, the continuous production of gutturals might enhance the coordination of flocks and spacing between individuals.

Guttural calls could be regarded as complex vocalizations. Complexity comes not only from structural diversity but also from the way in which vocal elements are combined (Smith 1997). Blue-fronted Amazons might use a combination of gutturals and other calls (*wakwak* and *wawawawa*) as a means of increasing the information contained in single guttural notes. Similarly, songs of Blue-fronted Amazons are formed by combinations of different calls with specific syntax rules (Fernández-Juricic et al. 1998c). Similar composite vocalizations with the arrangement of notes varying according to the context of vocalization have been found in other species (Hailman et al. 1987, Armstrong 1992), and could be important for aggregation during the non-breeding season.

The complexity of auditory signals may be greatly influenced by acoustic characteristics of the habitat and ultimately may affect social relationships. Close range signals are not influenced by as many acoustic restrictions as long range sounds (Marler 1967, Wiley and Richards 1982, Forrest 1994). Blue-fronted Amazons' guttural calls appear to serve as close range signals because of their large variability, broad bandwidth, short duration, rapid repetition, abrupt onsets, low intensity, and frequency modulation patterns. These characteristics would greatly limit the distance at which guttural calls could be detected. Because they are low intensity, they probably evolved to transmit messages across relatively short distances, such as contact situations (Wiley 1976). This sort of vocalization usually takes place in large social groups (Marler 1965), such as in this species' large flocks. Similar close range vocalizations have been

encountered and simulated in Black-capped Chickadees (Clemmons 1997).

Given the high degree of acoustic variation coupled with the isolation of the population we studied, it could be predicted that Blue-fronted Amazons' guttural calls would vary between distinct populations, producing local variations or dialects (Krebs and Kroodsma 1980). Such local variability has been found in other *Amazona* parrots, such as *A. auro-palliata* (Wright 1996). Future research should be oriented towards studying the guttural calls of other Blue-fronted Amazon populations to identify possible dialects.

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